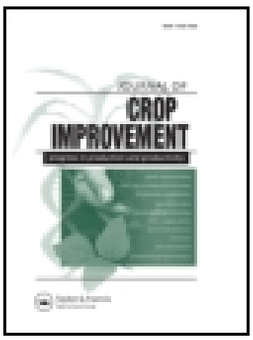

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Genetic and genomic resources for finger millet improvement: opportunities for advancing climate-smart agriculture

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ABSTRACT

Finger millet (FM; *Eleusine coracana* (L.) Gaertn.) is becoming increasingly vulnerable to various climate-induced stresses, because of which the genetic and genomic resources will be important for improving the crop in the 21st century. Currently, sizable-untapped genetic resources exists that offer promise for FM improvement to biotic and abiotic stresses. Also, earlier reports elaborate on the potential FM genomic resources, such as molecular markers, genetic maps, and DNA sequence, but the data are scanty to support the efficient and accelerated delivery of the climate-smart FM varieties. This is partly attributable to the delayed availability of complete genome sequence (CGS) of FM. Following the latest developments in FM genomic research, based on the CGS, a diversity of genomic resources have been reported. The review, therefore, provided a detailed analysis on the FM genetic and genomic resources-aided interventions that could contribute to the three pillars of Climate-smart agriculture (CSA) for addressing FM production challenges under changing climate. Exceptionally, it presented enriched information on additional useful sources of variation within FM genetic resources that have been screened for improving FM tolerance to various climate-induced stresses. Also, it presents the novel opportunities for CSA that could come as a result of the recent availability of CGS data for revolutionizing the development of cutting-edge-molecular breeding tools. Specifically, emphasis was placed on genome-wide-based technologies, such as genomic selection (GS), gene pyramiding, and gene expression with the second-generation genomic biotechnologies, such as TILLING and EcoTILLING that are wanting and have received little attention.

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Introduction

Finger Millet (FM) (*Eleusine coracana* (L.) Gaertn.) is a C4 crop that is envisioned to play a key role in CSA and boost food production in the face

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of climate change, especially in the developing world (Goron et al. 2015; Gupta et al. 2012; Bandyopadhyay, Muthamilarasan, and Prasad 2017). This low-input orphan crop (Goron et al. 2015; Bandyopadhyay, Muthamilarasan, and Prasad 2017) has evolved across 5000 years with subsistence farmers majorly in Africa and Asia (Dida and Devos 2006; Fuller and Hildebrand 2013). It serves as a food-security crop because of its high nutritional value and excellent storage qualities (Chandra, Chandra, and Sharma 2016; Ramashia et al. 2018). Finger millet grain is gluten-free, rich in calcium, fiber, iron, and methionine, tryptophan, and other essential amino acids, with excellent malting qualities, and has a low glycemic index (Chandra, Chandra, and Sharma 2016; Pandian et al. 2017). More importantly, FM grain contains higher calcium than other cereals (Kumar et al. 2016), and it is also endowed with abundant phytochemicals, with distinguished health beneficial properties, making the crop a reservoir of health-giving nutrients (Chandra, Chandra, and Sharma 2016).

Cumulative evidence shows that the growth and productivity of FM is becoming gradually vulnerable to various climate-induced biotic (pest, pathogens) and abiotic (solar radiation, drought, temperature, salinity) stresses (Gupta et al. 2017; Pavan et al. 2018). Climate change is happening so quickly on a global scale, and it is evident that in the last few decades, global agriculture has experienced increasing vulnerability because of erratic weather patterns, especially increased temperature and water stress (FAO 2011; IPCC 2014, 2018). The rising CO_2, coupled with other GHGs, majorly resulting from anthropogenic activities, is estimated to have caused approximately 1.5°C of global warming above the pre-industrial levels (IPCC 2018). In the future, the warming is likely to range between 3.7 and 4.8°C by 2100 (IPCC 2014), and further exacerbate agricultural production risks (IPCC 2014; Pavan et al. 2018).

Studies affirm that with a temperature rise of 2°C or more, without mitigation, production of the cereal crops will be negatively affected in the tropics (Niang et al. 2014; IPCC 2014). According to Jena and Kalli (2018), like any other crop, most biological processes in FM are also temperature-sensitive. Plant growth could diminish in situations where the temperature is below 8°C or above 36°C. Additionally, the rising CO_2 indirectly impacts plant performance through its effect on air temperature and water stress as well as directly by affecting plant metabolism through its role in photosynthesis (Kanwal et al. 2014; Abebe et al. 2016). In general, climate change is already influencing the distribution of land suitable for cultivating many crops, thus significantly contributing to decreased productivity of most agricultural systems, especially for the resource-poor farmers (Adhikari et al., 2015). Furthermore, considerable evidence shows that the amount of land suitable for cereal crop production, including FM, will decline across the

world because of exacerbating abiotic stresses, in particular drought, salinity, and heat (Maqsood and Ali 2007; FAO 2015; Sudan, Negi, and Arora 2015).

Coping with the intensifying climatic challenges will necessitate adaption of new crop varieties that are tolerant to drought, high temperatures, flooding, salinity, and other environmental extremes. Consequently, the vital diverse FM genetic and genomic resources will become the core for strengthening the crop's resilience to the adverse climatic conditions through climate-smart plant breeding in the 21st century (FAO 2015; Bandyopadhyay, Muthamilarasan, and Prasad 2017). The article, therefore, provides the latest knowledge on how the FM genetic and genomic resources could contribute to a transition to CSA to ensure increased and sustainable FM production in the face of climate change. It is intended to provide improved information on the additional screened FM germplasm base that is available for climate-smart breeding. Also, an updated detail on cross-compatibility, distribution, and genetic diversity of FM genetic resources for climate-smart breeding has been provided. Furthermore, expanded knowledge has been provided on the putative strategies for the implementation of genome-wide breeding research under the availability of the high-quality FM CGS data within the framework of CSA.

Climate-smart agriculture

Ensuring increased and sustainable FM production in the face of climate change requires a transition to agricultural production systems that are resilient to climate risks and shocks. Additionally, they should contribute to climate change mitigation and preservation of the vital ecosystem services (FAO 2011; Tumwesigye et al. 2019). Climate-Smart Agriculture (CSA) is the latest approach built on the grounds and experience of sustainable development that has attained recognition in addressing agricultural challenges under changing climate (Amin et al. 2015; Tumwesigye et al. 2019). This is achieved through its three dimensions namely; 1) Sustainable increase of agricultural productivity and incomes while conserving biodiversity, 2) Adapting and building resilience to climate change, and 3) Climate change mitigation – reducing greenhouse gas emissions (Amin et al. 2015).

Plant genetic resources constitute the base materials for crop improvement to withstand climate-induced biotic and abiotic stresses (FAO 2015). In contrast, genomic resources are genome-aided tools that accelerate the creation of climate-smart crop varieties (Bandyopadhyay, Muthamilarasan, and Prasad 2017; Ceasar et al. 2018). Utilization of the FM genetic and genomic resources is one of the pathways to the CSA approach that could provide sustainable and cost-effective options that are crucial for increasing long-term crop productivity. Since FM is grown at subsistence level in marginal areas, this could lead to the required adaptation and mitigation options that

could ensure sustainable food and income security while preserving the agro-ecosystem services.

Finger millet gene pool and distribution of genetic diversity for climate-smart breeding

Amid increasing and unpleasant climatic conditions, next-generation breeding for climate-resilient cultivars of FM will rely largely on wide-scale identification of adaptation traits available in diverse populations and germplasm collections. The cultivated FM (*Eleusine coracana* subsp. *coracana; 2 n = 4x = 36*) is a likely product from the selection and domestication of a large-grained mutant of the wild *E. coracana* subsp. *Africana*, which is native to Africa but exhibits wider distribution to semi-arid parts of the world, especially Asia and South America (Dida et al., 2008; Fuller et al. 2011; Fuller and Hildebrand 2013; Dida and Devos, 2006). Hence, the continued existence of landraces, together with wild relatives, in diverse agro-ecosystems, presents the opportunity for immense and distinct evolutionary adaptive genetic variations. This could offer huge opportunities for either selection or development of climate-resilient cultivars with stable yields and adaptation to abiotic (e.g., drought) and biotic (e.g., pests and diseases) stresses.

The national and international breeding programs are already seeking to develop new FM varieties that will be well adapted to climate-induced stresses. This is likely to increase the demand for a range of millet germplasm, including those of the crop wild relatives. The natural distribution of the wild relatives is restricted to two centers of diversity with sufficient variations, which include the highly variable primary center of origin in Africa and a secondary center in India (Fuller and Hildebrand 2013; Onziga, 2015; Tesfaye and Mengistu, 2018). Both the wild *E. africana* (2 n = 4x = 36; AABB genome) and cultivated FM *E. coracana* (2 n = 4x = 36; AABB genome) are important from the standpoint of germplasm collection and conservation, as they form the primary gene pool that is freely cross-compatible. Similarly, the cultivated FM is cross-compatible with another allotetraploid, *E. kigeziensis* (2 n = 4x = 38; AADD genome), which is also confined to the African continent with high endemicity in eastern Africa (Dramadri. 2015). The cross-compatible diploid wild species *E. indica* (2 n = 2x = 18; AA genome), *E. floccifolia* (2 n = 18; BB genome), *E. tristachya* (2 n = 18; AA genome), and *E. intermedia (*2 n = 18; AB genome) form the secondary gene pool. The tertiary gene pool comprises diploid species *E. jaegeri* (2 n = 2x = 20; DD genome), *E. multiflora* (2 n = 2x = 16; CC genome), and *E. verticillata* (2 n = 2x = 18). Additionally, it has been comprehensively established that the diploid *E. indica* (wild goosegrass) is the source of the A genome in FM, but wanting evidence still exists on the source of B genome (Devarumath et al. 2005; Liu

et al., 2014; Hatakeyama et al. 2018; Zhang et al. 2019). Nevertheless, research on those species could bring novel genes that can be introgressed into the cultivable FM to develop high-yielding and stress-tolerant varieties, particularly against extreme drought, heat, salinity, low nutrients, and the devastating FM blast disease, all exacerbated by climate change.

Sources of finger millet germplasm that confer tolerance to climatic stresses

More than 34,675 FM accessions are available in the major gene banks at various international and national research organizations worldwide (Dwivedi et al. 2012). More importantly, many of these are cross-compatible with the domesticated species, which offer greater opportunities for improvement for tolerance to the climatic stresses (Dwivedi et al. 2012; Saha et al. 2019; Gupta et al. 2017).

Unfortunately, the size of the collection with a promising genetic diversity has limited uses because of the costs associated with screening all accessions for traits that could be used in crop improvement programs. However, to maximize the usefulness of the conserved germplasm, preliminary screening attempts have been initiated by scientists. Core collections of 622 (Upadhyaya et al. 2005), and a mini-core collection of 80 accessions (Upadhyaya et al. 2010; Babu et al. 2013) have been developed based on phenotypic characterization and multi-locational evaluation data recorded for quantitative traits.

The evaluations have identified useful variations, leading to availability of germplasm that is early maturing, high yielding, blast-resistant. In addition, a few drought- and salinity-tolerant accessions have been identified, which can be utilized in hybridization programs for strengthening FM resilience to climatic stresses. The blast-resistant accessions belonged to one wild (*E. africana*) and four cultivated (*E. Coracana*) races (*vulgaris, plana, elongate,* and *compacta*), and also possessed significant diversity for agronomic traits, such as maturity period, plant height, and panicle type. Similarly, many accessions with grains having high protein, calcium (Ca), iron (Fe), and zinc (Zn) were also identified that can be used to enrich the cultivated FM and other crops with increased nutrient levels (Babu et al. 2013).

In addition to the core and mini-core evaluations, in the last few years, gradual research attempts commenced at various research institutions to identify or develop FM genotypes with tolerance to climatic stresses (Table 1). So far, a few classical breeding programs in countries, such as India, Malawi, Zimbabwe, Kenya, Tanzania, and Ethiopia, have bred and released varieties with improved yield and tolerance to climatic stresses (Lenne et al. 2007; Mgonja et al. 2011; Sreenivasaprasad et al. 2004). These improved genotypes and screened materials could provide additional

Table 1. Screened finger millet germplasm base available for climate-smart breeding.

Traits and accessions	Country	Reference
Blast resistance trait		
NW Himalayan, VHC3997, VHC3996 and VHC3930, IE-4795, VL-149, DM-7, PR-202, GPU-76, VR-948, BR-2, TNAU-1063, RAU-8, TNAU-1066, GPU-67, OEB-532, PPR-2885, and IE-4709	India	Babu et al. (2014); Ramakrishnan et al. (2016); Ganesha et al. (2018); Saha et al. (2019)
KNE 688, KNE 814, KNE 1149, P 224 (Pese 1), Seremi 1, Seremi 2, Gulu E, SX8, SEC 915, KNE 409, KNE 1098, KNE 409, and 1098	Kenya Ethiopia Uganda	Lenne et al. (2007); Mgonja et al. (2011); Sreenivasaprasad et al. (2004)
Drought and salt tolerance traits		
ML 181, ML-365, IE 4797, PR202, MR1, GPU28, and Trichy 1	India	Hittalmani et al. (2017); Rahman et al. (2014); Hatakeyama et al. (2018) Singh et al. (2014b)
High proteins, calcium, iron and zinc level traits		
GE-6834-1, VL-384, GE-728, VR-1034; JWM-1, VR-1034, OUAT-2, TNEC-1234, GPU-71, VR-936, GPHCPB45, GPHCPB44, IE2957 and IE6537, GP-45 GPHCPB-17, GPHCPB-20, GPHCPB-21, GPHCPB-26, GPHCPB-33, GPHCPB-35, GPHCPB-36, GPHCPB-37, GPHCPB-40, GPHCPB-42, GPHCPB-44, GPHCPB-45, and GPHCPB-52	India	Saritha (2015); Yadav., Kumar., and Thakur (2017); Akbar et al. (2018); Panwar et al. (2010); Chinchole et al. (2017)
Phosphorus starvation tolerance traits		
GPU45, IE5201, IE2871, IE7320, GPU66, HOSUR1, TCUM1, IE2034, SVK1, RAU8, VR708, and IE3391	India	Ramakrishnan et al. (2017)
Nitrogen starvation tolerance traits		
GE-3885	India	Gaur et al. (2018); Kanwal et al. (2014); Gupta et al. (2018)
Aluminum toxicity tolerance trait		
Gute and Degu	Ethiopia	Brhane et al. (2017)

useful sources of variation to the existing hub of germplasm in gene banks that confer tolerance to various climatic stresses for climate-smart breeding.

Furthermore, exploitation of the induced and natural mutant lines in the future could lead to the broadening of the genetic base for FM improvement against multiple climatic stresses. However, the mutant genetic resources available for FMs are negligible (Saha et al. 2016), which require additional attention. Generally, little has been done concerning the identification of sources of tolerance to abiotic stresses, such as drought, salinity, aluminum toxicity, nutrient starvation, waterlogging, and heat stress in FM. Besides, most of the reported screening trials were generally based on phenotypic data. Thus, the recent development in FM genomics research is expected to provide vibrant support for accurate and accelerated screening of the available FM genetic resources for tolerance to various stresses. Ultimately, this will enhance the breeding efficiency of research programs, and hasten the creation and provision of climate-smart FM varieties for CSA.

Genomic resources available for enhancing finger millet resilience to climatic stresses

Based on the NCBI database (https://www.ncbi.nlm.nih.gov/), in general FM has narrow genomic resources as compared with other major cereals, which hamper further improvement of this crop. As reported by Ceasar et al. (2018), FM has only 1934 ESTs associated with drought, salinity, and disease-tolerance traits. These are approximately 662.4, 1046.3, and 434.5 times less compared with rice, maize, and barley, respectively. Nevertheless, within grasses, comparative genomics has been well studied, and can contribute considerably to marker-assisted selection efforts for tolerance to numerous climatic stresses in FM (Yadav et al. 2014; Ramakrishnan et al. 2016, 2017; Hittalmani et al. 2017; Pandian et al. 2018). The EST projects have yielded a vast amount of sequence data for other grasses that are publicly available at the NCBI Genbank database. With the help of bioinformatics tools, SSRs could be mined through *in-silico* synteny analysis across the grass genomes.

Studies have also revealed high transferability of genic SSR markers associated with tolerance to climatic stresses and superior agronomic traits, such as blast tolerance, Ca, and yield among grasses, including FM (Yadav et al. 2014; Ramakrishnan et al. 2016). Such transferability of genomic resources from other well-studied grasses to FM, supported by the extensive gene-level synteny shared between the grass genomes, could be useful for improving the less-studied orphan crop for many complex climatic stresses.

Using Roche 454 and Illumina Next Generation Sequencing (NGS) technologies, 10,327 SSRs, and 23,285 non-homeologous first SNPs were reported in FM (Gimode et al. 2016). Furthermore, following the recent whole-genome research development for FM (Hittalmani et al. 2017), ample genomic resources with numerous opportunities for CSA have been reported. This wealth of high-quality genomic data that include among others 114,083 SSRs, 1766 R-genes, 2866 drought-responsive genes, 146 C4-pathway genes, 56 families of transcription factors (TFs), and 330 calcium transport and accumulation-related genes also exists at the NCBI Genbank database for public use. Possibly, it could serve as a reference for modernizing FM molecular research in the future.

Prospects for the development of climate-smart finger millet varieties using genome-aided tools

Even though conventional breeding approaches have continued to contribute to genetic improvement of important traits in FM, their efficiency can be increased considerably by supplementation with genome-aided breeding

tools. However, the absence of FM CGS hampered the needed paradigm shift with respect to molecular-marker development, diversity assessment, linkage-map construction and quantitative trait locus/loci (QTL) mapping (Upadhyaya et al. 2010; Dwivedi et al. 2012; Saha et al. 2019; Gupta et al. 2017). As a result, the breeding progress, for improving tolerance to climatic stresses, has been slow and difficult for this orphan crop. Nevertheless, comparative genomic studies within grasses, have contributed primarily to the development of molecular marker systems that could be exploited for climate-smart breeding in FM. Thus, we update on the available potential key markers/QTL and candidate genes that could support climate-smart molecular breeding.We also highlight the prospects for the implementation of genome-wide breeding research under the availability of the high-quality FM CGS data in the context of CSA.

Potential molecular tools for genetic diversity and population structure analysis for enhancing climate-smart breeding in FM

Development of climate-smart cultivars could require introgressing stress-tolerance traits into various genetic backgrounds. Therefore, accurate assessment of genetic diversity and population structure for the vast amount of FM germplasm maintained in gene banks worldwide is crucial for genetic resource management, trait mapping, and crop improvement. A few studies have attempted to exploit molecular tools for the analysis of genetic diversity and structure in the landraces, collections, and wild germplasm accessions of this orphan crop (Table 2). The findings provide foundation knowledge about the level of polymorphism exhibited by the different markers for discerning useful variation among FM genotypes that could be exploited in breeding programs against various climatic stresses. For instance, various FM genotypes from cultivated and wild germplasm have been identified as most diverse parents that could generate high-vigor cultivars through hybridization. The genotypes harbor novel genes that hold potential for improving FM for Ca accumulation, variable seed-coat color, high grain-nutrient content, blast-resistance and drought-tolerance traits (Gupta et al. 2010; Panwar et al. 2010; Babu et al. 2014; Dramadri. 2015; Saha et al. 2019). These genotypes could be exceptionally used as parental lines for developing climate-smart cultivars.

In general, almost all the past diversity-assessment studies were based on PCR and EST markers that were mined through *in-silico* analysis (Table 2). These markers could have some limitations, as the development of accurate primers, in the absence of complete genomic information, is quite difficult (Garibyan and Avashia 2013: Khar and Saini 2016). Additionally, a limited number of genotypes have been analyzed for a few traits, and the number of markers available for diversity analysis is still small. Application of the raw

Table 2. Potential molecular markers for genetic diversity analysis available for accelerating climate-smart breeding in finger millet.

Marker type†	Number of markers	Number of genotypes	Polymorphic information content (PIC)		Source of germplasm	Marker opportunities for climate-smart agriculture (CSA)	References
			mean	Range			
Genic SSRs	58	190	0.385	0.186–0.677	India	Selection of blast-resistant genotypes	Babu et al. (2014)
SSRs	19	340	0.606	0.035–0.889	Kenya Uganda Tanzania	Selection of diverse parents for hybridization	Manyasa et al. (2015)
SSRs	20	105	0.53.	0.09–0.88	Uganda	Selection for drought-tolerant and diverse parents for hybridization	Dramadri. (2015)
RAPD	10	3	0.348	0.11–0.51	India	Selection of FM genotypes with variable seed coat color	Gupta et al. (2010)
ISSR	10	3	0.193	0–0.39	India		
EST-SSRs	3	48	0.717	0.674–0.766	Zimbabwe Uganda Kenya Malawi India Nepal	Selection of diverse parents for hybridization	Obidiegwu, Parzies, and Obidiegwu (2014)
RAPD	18	52	0.351	-	India	Selection of FM genotypes with high Ca content and diverse parents for hybridization	Panwar et al. (2010)
SSRs	10	52	0.505	-	India		
Cytochrome P450	10	52	0.406	-	India		
SRAP	12	67	0.243	0.116–0.459	India	Selection of blast resistant genotypes and diverse parents for hybridization	Saha et al. (2019)
SSR	12	67	0.252	0.076–0.384	India		
SSR	20	72	0.80	0.46–0.91	Ethiopia	Selection of cross- compatible and diverse parental lines for hybridization	Dagnachew et al. (2014)
Genomic SSRs	49	10	0.42	0.16–0.77	Tanzania Kenya Uganda Ethiopia	Selection of cross- compatible and diverse parental lines for hybridization	Gimode et al. (2016)
SNP	80	89 (30 wild and 59 cultivated accessions)	0.29	0.01–0.38	ICRISAT‡ Tanzanian and Kenyan Gene Bank		Gimode et al. (2016)
SSR RAPD ISSR	21 12 2	2 acesssions	All the markers were polymorphic		India	Selection of drought tolerant genotypes and diverse parental lines	Krishna et al. (2020)

data of the current genome is expected to explode and modernize a systematic and accurate analysis of the diversity existing within cultivated and wild FM germplasm. To this end, the complete genome will provide a strong platform for mining highly informative genomic markers, such as SSRs and SNPs. These could be increasingly used as next-generation markers of choice for accurate genotype identification and diversity analysis in FM, as done in other major cereals (Samayoa et al., 2015; Zhang et al. 2016; Pavan et al. 2018). Actually, this will help to inform sound breeding programs and define suitable genotypes with superior alleles that meet the breeding demands.

Identification of QTL associated with climatic stress tolerance traits

The majority of the traits that confer tolerance to climatic stresses such as disease, drought, salinity, nutrient starvation tolerance are complex and governed by QTL (Ceasar et al. 2018; Ramakrishnan et al. 2016, 2017; Serba and Yadav 2016; Sharma et al. 2014; Yadav, Sehgal, and Vadez 2011; Yadav et al. 2014). Hence, genetic improvement of such traits can be achieved through marker-assisted breeding once the QTL are identified and mapped.

At present, largely, the resistance genes (R-genes) are not yet mapped in FM. A few studies have, however, mapped R-genes for blast disease that were based on *in-silico* analysis (Table 3). According to Babu et al. (2014), four QTL for finger blast resistance and one for neck blast resistance were reported through association mapping using 104 SSRs to screen 190 FM genotypes via the general linear model (GLM) approach. Likewise, via the mixed linear model (MLM) approach, seven markers were associated with QTL for blast disease resistance; 3 with leaf, 1 with neck, and 3 with finger blast. Both the GLM and MLM approaches revealed three common markers, i.e., RM262, FMBLEST32, and UGEP18 that were linked to blast disease resistance QTL. The markers explained 5–13% phenotypic variance (R^2), and were concentrated on chromosomes 1B, 2A, 3B, 4B and 6B of FM. Probably, these represent the major hub of finger blast and neck blast resistance genes. In a subsequent association mapping study using 87 genomic SSR markers, 128 FM germplasm collections, originating from major diversity centers both in India and abroad, were analyzed. A total of seven QTL were found to be associated with various agronomic traits, including leaf blast resistance (Ramakrishnan et al. 2016). Two markers (UGEP101 and UGEP95) were strongly associated with leaf blast resistance QTL, and explained 21.05 and 8.95% phenotypic variation respectively.

This preliminary information on blast resistance QTL, along with the associated markers, could be useful for the development of climate-resilient genotypes with high resistance to blast disease and acceptable agronomically

Table 3. Details of markers associated with climatic stress-tolerance and superior agronomic traits for climate-smart breeding.

Trait	Marker	Phenotypic variance explained (%) (R^2)	Chromosome	Reference
Finger blast	RM262	5–10	2A	Babu et al. (2014)
	FMBLEST32	4.5–8	6B	
	UGEP81	7.50	6B	
	UGEP53	10.50	-	
	UGEP24	8.00	3B	
Leaf blast	FMBLEST35	10.00	4B	
	FMBLEST15	8.00	4B	
	RM23842	11.00	6B	
Neck blast	UGEP18	11–13	1B	
Leaf blast	UGEP101	21.05		Ramakrishnan et al. (2016)
	UGEP95	8.95		
Plant height	UGEP50	6.69		
Number of tillers	UGEP98	9.53		
	UGEP65	11.72		
Number of productive tillers	UGEP98	7.00		
	UGEP65	7.00		
	SSR01	6.51		
Number of fingers	UGEP104	6.85		
	UGEP75	6.31		
Length of root	UGEP9	8.12		
	UGEP57	6.28		
Seed yield	UGEP9	10.71		
	UGEP19	7.63		
	UGEP80	6.78		
Ca accumulation	UGEP78		1B	Yadav., Kumar., and Thakur (2017)
	UGEP60			
LRDW†	UGEP19	9.5–14.3		Ramakrishnan et al. (2017)
	UGEP68	6.5–10.6		
HSDW‡	UGEP13	12.7		
HRL§	UGEP90	9.2		

superior traits through marker-assisted QTL introgression. However, the markers were developed through *in-silico* analysis using primers designed from the *Magnaporthe grisea* (rice blast fungus) genes and several cloned rice blast *Pi* genes (Babu et al. 2014). Therefore, for the next-generation breeding, the arrival of the complete FM genome is expected to be a resource for fine mapping and validation of these QTL, along with the associated genic markers. Indeed, it will shorten the breeding for climate-smart cultivars, especially with high resistance to blast disease and acceptable agronomic traits. Resistance to the devastating blast disease exacerbated by climate change could minimize chemical use and lead to reduced emission of GHGs as well.

Finger millet is specifically Ca-rich compared to other cereals (Kumar et al. 2016). It is also a locally well-adapted semi-arid crop that is expected to drive food security for the developing world under climatic change-related

stresses. Hence, the identification of QTL controlling nutrient signaling and Ca accumulation traits will be essential for improving FM shortly and enriching other cereals with elevated Ca levels. A total of 9 QTL associated with Ca content were identified in 113 genotypes of FM using 14 anchored-SSR markers that were designed from calcium transporters and sensors (Kumar et al. 2015). Through association analysis, using a global collection of 238 genotypes, and 85 genic and non-genic (SSR) markers, two genomic SSR markers (UGEP78 and UGEP60) were reported to be significantly associated with grain calcium content (GCC) (Yadav., Kumar., and Thakur 2017). UGEP60 marker is linked to QTL for GCC that belongs to linkage group 1B of finger millet, which is also syntenous with rice chromosome 1 harboring a QTL for calcium content. Though the identified QTL/markers could kick-start the genetic improvement of calcium content in finger millet, the availability of the complete genome is expected to contribute to the next generation advancement for fine mapping QTL associated with this trait. This could enhance successful genetic improvement of low-Ca FM genotypes and the other cereals under the stresses associated with climate change.

It has already been established that under extreme drought, uptake of nutrients, such as nitrogen (N) and phosphorous (P), in plants will be adversely affected (Goron et al. 2015; Gupta et al. 2012; Ramakrishnan et al. 2017; Bista et al. 2018). However, nutrient signaling breeding in FM has not yet been exploited partly because of the scanty molecular information about the QTL governing nutrient-uptake mechanisms. Based on association mapping of 128 FM genotypes from 18 countries two QTL (*qLRDW.1* and *qLRDW.2*) were found to be associated with root dry weight, under low P, using 72 SSR markers (Ramakrishnan et al. 2017). The same authors reported two other QTL, viz., *qHSDW.1* and *qHRL.1*, under P-sufficient conditions, which affected shoot dry weight and root length. The four reported QTL, viz., *qLRDW.1, qLRDW.2, qHSDW.1*, and *qHRL.1*, were linked to UGEP19, UGEP68, UGEP13, and UGEP90 markers, respectively (Table 3).

So far, a few QTL mapping studies related to nutrient signaling and accumulation have been conducted in FM (Ramakrishnan et al. 2017; Kumar et al. 2016). Under the changing climate scenario, a detailed understanding of nutrient deficiency QTL will be important for the development of low-nutrient-tolerant FM cultivars. Therefore, the complete-genome-aided research is expected to help in the precise detection of nutrient-starvation-tolerance QTL for MAS. Eventually, it will facilitate the selection of either cultivars for areas where nutrient deficiency is noticeable or germplasm lines that could be used as donors for nutrient-starvation-tolerance genes. Thus, this will help to enhance productivity and resilience of resource-poor farmers, especially with low purchasing power for expensive fertilizers, and simultaneously reduce GHG emissions through minimal fertilizer application.

Even though the highlighted foundation studies inform about the genetic loci associated with various climatic stresses, it is typically difficult to isolate candidate genes based on such few QTL-mapping experiments. The availability of the recent CGS will be instrumental in rapid validation, discovery, and fine mapping of QTL associated with complex stress-tolerance traits. The resultant high-density maps based on genome-wide next generation markers, such as SNPs and SSRs, could precisely facilitate the identification of genes, gene cloning, and gene pyramiding for improving traits that determine yield or/and confer tolerance to multiple climatic stresses in FM.

Linkage and association mapping are the two most common methods used for identifying QTL conditioning complex traits; through these methods genes/QTL have been identified in different plant species (Yang et al. 2011; Zhang et al. 2016; Lule et al. 2018; Sharma et al. 2018). Since the development of bi-parental mapping populations for small millets is a difficult, the classical linkage analysis of QTL for traits associated with climatic stresses is limited. Also, large mapping populations are required to achieve high-resolution maps. It could be presumed that the genome-wide association studies (GWAS) and genotyping-by-sequencing in FM could be ignited by the advent of the CGS. These could evolve as powerful second-generation biotechnological tools for high-resolution QTL mapping and SNP discovery in FM, as in other well-studied cereals, such as maize (Cappa et al., 2013; Samayoa et al., 2015; Zhang et al. 2016). Accordingly, this could lead to overcoming limitations associated with the traditional QTL-analysis approach.

In addition, the availability of genome-wide high-density markers that cover the whole genome could further provide opportunities to increase genetic gains for complex traits through genomic selection (GS). With the continuous decline in sequencing costs, coupled with the availability of high-throughput sequencing platforms, the next-generation marker technology could provide hope for the selection of superior FM genotypes based on accurate breeding values. Hence, these could constitute foundation breeding populations for developing climate-smart FM cultivars at a low cost under the current climate-change scenario.

Functional characterization of key genes associated with climate-change-induced stresses

Under the present situation, it has been understood that climate-change-induced stresses, such as diseases, drought, salinity, and aluminum toxicity, have a serious effect on nutrient uptake, assimilation, and carbon metabolism in plants (Maqsood and Ali 2007; Goron et al. 2015; Bista et al. 2018). These effects are expected to further exacerbate agricultural production risks

in the future. Therefore, considerable research attention, focusing on the identification of the candidate genes associated with climatic stresses for enhancing FM resilience, could contribute to the required adaptation strategies.

Finger millet, a C4 crop, has a higher calcium content than some other cereals (Kumar et al. 2016), and it is likely to have evolved unique mechanisms that permit the plant to perform well under low nitrogen and adapt to a wide range of environmental stresses, such as drought, salinity, aluminum toxicity, and diseases (Goron et al. 2015; N. Gupta et al. 2012; Bandyopadhyay, Muthamilarasan, and Prasad 2017). It is suggested that the genes underlying these complex mechanisms are driven by strong promoters, transcription factors, and regulatory proteins (Gaur et al. 2018; Pudake et al. 2017; Rahman et al. 2016; Ramakrishna et al. 2018; Ramegowda et al. 2012; Sharma et al. 2017; Singh et al. 2014a, 2015). However, a lack of comprehensive understanding of these underlying mechanisms, unlike in other well-studied cereals, such as rice, has been a bottleneck, especially because of availability of scanty genomic information. Nevertheless, based on model crops and comparative genomics, opening studies have been reported on the expression profile of some genes associated with stress tolerance, which could be used for climate-smart breeding (Table 4).

Most plants, including FM, obtain their mineral nutrients from the soil and transport them using nutrient-uptake proteins located in the cellular membranes of roots and shoots (Pudake et al. 2017; Sharma et al. 2017; Singh et al. 2014a, 2015). For instance, ammonium is taken up by the high-affinity AMT1family, while nitrate uptake is associated with members of the *NRT1* and *NRT2* families of transporters with low-affinity NO_3^- transporters at high N levels and high-affinity NO_3^- transporters at low N levels, respectively (Dechorgnat et al. 2010; Xu, Fan, and Miller 2012). Similarly, phosphorus (P) is taken up by roots via the activity of *PHT1*-type transport proteins (Varma et al., 2017; Pudake et al. 2017). Most of the genes expressed in roots are up-regulated in P-stressed plant for this *PHT1* family (Smith et al. 2003). Three ATP-binding cassette (ABC) (*LOC_ Os11g39020, LOC_Os02g32690, LOC_Os01g24010*) transporters and KUP (potassium uptake permease) potassium type transporters were reported by Rahman et al. (2014). The same authors reported several other transporters involved in the transport of various cations and anions, including metal cation transporter (*LOC_Os03g46470*) and proton antiporter-2 family (*LOC_Os11g42790*). These were significantly up-regulated in response to salinity stress in a tolerant FM genotype. This initial understanding of transport proteins forms a promising basis for crop improvement. In the future, their genetic manipulation under availability of FM CGS could be important in enhancing wide adaptation to soil nutritional, drought, and salinity stresses. For instance, wide-scale genome-aided alteration of sodium or potassium

Table 4. Candidate genes associated with stress tolerance available for finger millet (FM) improvement.

Candidate genes	Expression region	Potential sources	Opportunity for climate-smart agriculture	Reference
N uptake and assimilation				
EcHNRT2, EcLNRT1, EcNADH-NR, EcGS, EcFd-GOGAT, and EcDof1	All induced in leaves Except EcHNRT2 which induced in root	FM	Development of NUE varieties	Gupta et al. (2013)
Eca-prolamin gene	Root, stem, leaves and seedling stage	FM Barley	Development of NUE varieties	Gaur et al. (2018)
Genes Involved in Ca Transport				
CAX1, TPC1, *CaM-stimulated type IIB Ca2+ ATPase and two CaM dependent protein kinase (CaMK1 and 2)*	Root stem spike	FM Wheat Rice Barley Maize Sorghum	Enhancing Ca uptake and development of calcium biofortified crops	Mirza et al. (2014)
Ca sensor genes family *CaM and CaMLs, CBLs, CIPKs, CRKs, PEPRKs, CDPKs, CaMKs, and CCaMK.*	spikes	FM Rice Sorghum Maize	Developing Ca-biofortified crops	Singh et al. (2014b)
Ca transporter genes including *Ca2+ ATPases, Ca2+/cation ex- changers and Ca2+ channel*	Seed	FM Rice	Developing Ca-biofortified crops	Singh et al. (2015)
CIPk24	root, shoot, leaf and developing spike tissues	FM GP-45 Rice	Enhancing Ca uptake and developing Ca-biofortified crops	Chinchole et al. (2017)
Genes involved in carbon (C) metabolism				
Cab, RBCS, PEPC, PPDK, PEPC-k, ME, SPS, PK, 14-3-3 and SnRK1	Leaves of seedlings	FM Maize Barley Rice Wheat Sorghum	Selection of genotypes for better agronomic performance and Enhancing net CO2 assimilation in the near future.	Kanwal et al. (2014)
Genes involved in phosphate transport				
Four phosphate transporter genes (*EcPT1 to EcPT4*)	roots and leaves of seedling	FM Rice Maize	Improving FM tolerance to P starvation	Pudake et al. (2017)
Genes Involved in drought Stress Tolerance				
EcDehydrin7	Seedling	FM	Development of tolerant drought and heat crops	Singh et al. (2014b)

(*Continued*)

Table 4. (Continued).

Candidate genes	Expression region	Potential sources	Opportunity for climate-smart agriculture	Reference
RGAP2, DBH, GBF3, RSLP, HYP		FM Maize	Improved tolerance to osmotic stress, salinity, and drought stress	Ramegowda et al. (2017)
EcCIPK31-like	Leaves	FM Foxtail millet	Development of drought-tolerant crops	Nagarjuna et al. (2016)
Genes involved in salinity tolerance				
Vascular ATP synthase genes (*LOC_ Os03g14690, LOC_Os10g10500 LOC_Os04g55040*). Aquaporin proteins encoding genes (*LOC_Os02g57720, LOC_Os03g05290, LOC_Os07g26630, LOC_Os07g26690*) Other stress signaling genes *LOC_Os03g62180, LOC_Os07g03810, LOC_Os03g56270, LOC_Os07g35140, LOC_Os02g09740* *TKL_IRAK_DUF26* *LOC_Os11g26790*	leaves and shoots	FM Rice	Improving tolerance to salinity	Rahman et al. (2014)
BiP, PDIL, and CRT1	leaf, shoot, root, panicle, and germinated seedling	Tobacco FM Maize Rice	Development of salinity tolerant crops	Ramakrishna et al. (2018); Liu and Howell (2010)
LEA14, rd29A, rd29B, SOD, APX, ADH1, HSP70 and PP2C	seedlings	FM Sorghum Tobacco	Development of transgenic crops with tolerance to diverse stresses.	Babitha et al. (2015)

Table 5. Transcription factors associated with stress tolerance available for finger millet improvement.

Transcription factors	Expression sites	Source of gene	Opportunity for CSA	Reference
EcDof genes	root, stem, leaf, and developmental stages of spikes	FM Sorghum Rice	Development of nitrogen use efficient (NUE), biofortified varieties, and those adopted under increasing Co_2 for yield in the near feature	Kanwal et al. (2014); Gupta et al. (2018)
OPAQUE2 (O2) like TF	Root, stem, leaves, and seedling stage	FM Barley	Development of NUE varieties and biofortified crops	Gaur et al. (2018)
EcTAF6	Shoot, Root, seedling	FM Rice	improved salinity and drought tolerances	Parvathi et al. (2019)
EcbHLH57	leaves	FM Sorghum	Development of salinity and drought stress crops	Babitha et al. (2015)
EcNAC67 TF	leaves, root, and shoot tissues	FM Rice	Improved salinity and drought tolerances	Rahman et al. (2016)
EcGBF3		FM Maize	Improved tolerance of plants to osmotic stress, drought, and salinity	Ramegowda et al. (2017)
EcNAC1	Leaves	FM Rice Sorghum	Improved tolerance of plants to osmotic stress, drought, and salinity	Ramegowda et al. (2012)
NAC 67, bZIP, WRKY29 AP2, MYB and NAM family transcription factors	leaves and shoots	FM Rice	Improved tolerance of plants to osmotic stress, drought, and salinity	Rahman et al. (2014)
EcbZIP17	leaf, shoot, root, panicle, and germinated seedling	FM Rice Maize	Development of salinity and heat stress-tolerant crops	Ramakrishna et al. (2018)
bHLH (TF)	Root	*Brachypodium distachyon* Rice Foxtail millet	Development of P-starvation-tolerant genotypes	Ramakrishnan et al. (2017)
WRKY (TF)	Root	*Brachypodium distachyon* Rice Foxtail millet	Development of P-starvation-tolerant genotypes	Ramakrishnan et al. (2017)

transporters to improve tolerance to salinity, aluminum (Al) transporters to increase tolerance to Al toxicity, and nitrogen and phosphorus transporters for enhancing nutrient-starvation tolerance could contribute to the development of climate-resilient FM genotypes.

Additionally, the expression patterns of genes involved in nutrient signaling and response to abiotic stresses, such as drought and salinity, are primarily regulated at the transcriptional level by the promoter and several motifs recognized by plant-specific transcription factors (Table 6). These largely regulate the expression of multiple downstream target genes under stress conditions (Rahman et al. 2014). Preliminary reports on a few transcription factors (TFs) associated with climatic stresses in FM are listed in Table 6. In addition, the current published complete FM genome sequence possesses numerous transcription factors involved in nutrient signaling and response to abiotic stresses (Hittalmani et al. 2017). Consequently, the wealth of TFs housed by the currently released CGS could provide additional potential tools for manipulating stress tolerance in FM. These could further enhance studies to identify important pathways for the accumulation of diverse protective osmolytes, such as proline, associated with physiological response to osmotic stress caused by drought or salinity (Aleksza et al. 2017; Khatoon and Singh 2016). For instance, under adverse conditions, proline, which is regulated by the MYB type transcription factors PHR1 and *PHR1-LIKE1* (PHL1), acts as an osmoprotectant, stabilizing cellular structures and enzymes, scavenging reactive oxygen species (ROS), and maintaining redox equilibrium (Sudan, Negi, and Arora 2015; Aleksza et al. 2017). Indeed, such benefits could shrink GHG emissions from fossil fuel-dependent agricultural activities, such as irrigation, and inorganic fertilizer production.

In general, most of the previous expression-profiling studies for FM were based on model crops, such as *Arabidopsis thaliana*, rice, and tobacco. The introduction of CGS data could serve as an anchor resource that could stimulate similar studies as those on model plants. It is expected to provide novel opportunities for the rapid translation of genetic information through

Table 6. Cloned functional genes associated with stress tolerance traits in finger millet.

Genotype	Gene name†	Promoter/reporter	Purpose	Reference
GPU28	*PgNHX1 and AVP1*	CaMV35S GUS‡	Salinity tolerance.	Jayasudha et al. (2014)
GPU28	*mtlD*	CaMV35S GUS	Drought/Salinity tolerance.	Hema et al. (2014)
GPU 45	*chi11*	Maize ubiquitin promoter	Leaf blast disease resistance	Ignacimuthu and Ceasar (2012)
20 genotypes were used	*pPin 35S*	CaMVs35S	Leaf blast disease resistance	Latha, Rao, and Reddy (2005)

comparative genomic analysis between FM and closely related crops or other less-studied cereals. This will ultimately contribute to the required adaptations through crop diversification.

With the advent of complete genome raw data, gene-analysis studies could be aided with reverse genetic mutagenesis-based second-generation genomics biotechnologies including TILLING (Kashtwari, Wani, and Rather 2019), EcoTILLING (Bajaj et al. 2016), and other cutting-edge scientific tools, such as CRISPR/Cas9 (Miglani 2017). These non-transgenic reverse-genetics approaches are expected to have a broader application to plant species regardless of ploidy level or genome size (Barkley and Wang 2008). In the near future, they could serve as climate-smart high-throughput breeding tools for developing either stress-tolerant FM mutant parental lines or varieties on a short-time scale and at a low cost for CSA.

Largely, the recent advances in FM genomic research could guide or support genome-wide transcript profiling, functional diversity studies, and validation of candidate genes associated with climatic stresses; especially so, those involved in different nutrient signaling pathways, such as calcium, phosphorous, and nitrogen uptake genes, nitrogen and carbon metabolism genes, and abiotic stresses (drought, salinity). As FM is richer in calcium content compared to other cereals (Kumar et al. 2016), the identified calcium genes of the complete genome will help in exploring FM germplasm for calcium uptake, translocation, and accumulation in various tissues, and enrichment of other cereals with this vital nutrient.

Genetic transformation

Under the adverse climatic conditions, genetic transformation will be central to most crop improvement programs to address complex climate-induced stresses, as conventional methods could be hindered by limited genetic variability among cross-compatible germplasm. For FM, the exploitation of genetic transformation for climate-smart breeding is still in infancy, majorly because of impairments that have been associated with the lack of ample genomic resources (Hittalmani et al. 2017). So far, few transformation studies have been attempted to transfer genes associated with tolerance to leaf blast disease, drought, and salinity in FM (Table 6). This has been mainly because of the nonexistence of optimal transformation protocols for generating mutant lines in FM based on an *Agrobacterium*-mediated versatile method of gene delivery (Ceasar and Ignacimuthu 2014). Likewise, most previous transformation studies relied on Biolistic-mediated gene delivery and were limited to marker gene expression assessments using model plants (Latha, Rao, and Reddy 2005; Ceasar and Ignacimuthu 2014). In contrast, for other well-studied cereals, such as rice, *Agrobacterium*-mediated transformation has registered tremendous progress (Beyer et al. 2002; Zhang et al. 2016).

Outspreading these efforts to FM within a short time under the genomic era is a requirement to ensure improved food and economic security, as the crop is mainly grown by resource-poor farmers, mostly in semi-arid areas.

The availability of the complete genome assembly for FM is expected to enhance the *Agrobacterium*-mediated transformation protocols for the development of climate-resilient FM transgenic varieties. This is particularly so in equipping T-DNA with plant-specific promoters and terminators for cases where the genes of interest are from prokaryotes or non-plant eukaryotes. In general, the recent resources of the CGS for this orphan crop will serve as a reference for efficient, large-scale identification and cloning of additional foreign stress-tolerance genes from mutations based on SNPs in various transformation studies for enhancing FM resilience to multiple climatic stresses.

Conclusion

Finger millet is vulnerable to the intensifying climatic risks, though it has been considered a climate-resilient crop that could drive food production for the developing world in the 21st century. Ensuring increased and sustainable FM production in the face of climate change requires a transition to CSA production systems that are resilient to climate risks. Wise use of FM genetic and genomic resources through climate-smart breeding is one pathway that could significantly contribute to transition to CSA. Therefore, research initiatives should focus on trait-specific screening of the abundant FM genetic resources. This could aid in the identification of genotypes with superior alleles that meet the breeding demands attributable to increasing climate-induced stresses. Specifically, redesigning the climate-smart breeding research based on the recent wealth of the high-quality CGS data for FM is expected to revolutionize the discovery of high-throughput molecular breeding tools, such as SNPs on a large scale. The genome-wide-aided tools will support accurate diversity assessment, fine-mapping studies, genomic selection, and GWAS for enhancing marker-assisted breeding in FM. In addition, they could offer novel opportunities to enrich genetic transformation studies, and gene expression with second-generation genomic biotechnologies, such as TILLING, EcoTILLING, and CRISPR/Cas9, for developing climate-smart FM varieties. In general, assimilation of these genomic inputs could enhance the utilization of the assembled genetic resources and shorten the breeding time for climate-smart cultivars. Adoption of such climate-resilient FM cultivars for CSA will enhance long-term crop productivity while preserving the vital ecosystem services. Likewise, it could buffer crop production from the effects of greater climate variability and extreme events by reducing GHG emissions from direct and indirect agricultural activities that are heavily reliant on fossil fuels. Ultimately, this will lead to viable adaptation and

mitigation options, especially for the smallholder farmers with limited capacity to adapt under the current climate-change scenario.

Abbreviations

ABC	ATP-binding cassette
ADH1	*Alcohol dehydrogenase 1*
Al	Aluminum
AMT1	Ammonium transporter 1
AP2	*APETALA 2 gene farmily*
APX	*Ascorbate peroxidase*
AVP1	Arabidopsis vacuolar pyrophosphatase1
BiP	*Binding protein*
Bzip	*Basic leucine zipper gene family*
Ca	Calcium
Cab	*Chlorophyll a/b binding protein*
CaM	*Calmodulin gene*
CaM35S	Cauliflower mosaic virus 35s
CaMKs	*Calmodulin-dependent protein kinases*
CaMLs	*CaM-like genes*
CAX1= Cation exchanger 1;	
CBLs	*Calcium sensors calcineurin B-like*
CCaMK	*Ca2+/calmodulin-dependent protein kinase*
CDPKs	*Ca^{2+} dependent protein kinases*
CGS	Complete genome sequence
chi11	Rice chitinase
CIPKs	*CBL-interacting protein kinases*
CRISPR/Cas9	Clustered regularly interspaced short palindromic repeat)-Cas9
CRKs	*Cysteine-rich receptor-like kinases*
CSA	Climate-smart agriculture
DBH	*Dead/Death box helicase*
Dof	*DNA binding with one finger*
DUF26	*Domain of unknown function 26*
EcbHLH57	*Basic helix-loop-helix trancription factor 57*
EcDof =DNA binding with one finger from finger millet	
EcGBF3	*G-box-binding factor 3 from finger millet,*
EcNAC1	*NAM, ATAF1/2 and CUC2 domain protein transcription factor 1*
EcNAC67	*NAM, ATAF1/2 and CUC2 domain protein transcription factor 67*
EcoTILLING	Ecotype Targeting Induced Local Lesions IN Genomes
EcPT1 to EcPT4	*Phosphate transporters genes 1-4*
EcTAF6	*TATA-box binding protein associated Factor 6*
ESTs	Expressed sequence tags
ESTs	Expressed sequence tags
Fe	Iron
FM	Finger millet
GBF3	*G-Box binding factor3*
GHGs	Greenhouse gases
GLM	General linear model
GS	Genomic selection

(*Continued*)

(Continued).

GWAS	Genome-wide association studies
HRL	Root length under P-*sufficient* level
HSDW	Shoot dry weight under P-*sufficient*
HSP70	*Heat shock protein 70*
HYP	*Hypothetical protein*
ICRISAT	International Crops Research Institute for Semi-Arid Tropics
IRAK	*Interleukin-1receptor-associated kinase_*
ISSR	Inter simple sequence repeat
KUP	Potassium uptake permease
LEA14= Late embryogenesis abundant protein	
LRDW	Root dry weight under P-*deficiency* level.
MAS	Marker-assisted selection
ME	*Malic enzyme*
MLM	Mixed linear model
MtlD	Mannitol-1-phosphate dehydrogenase
MYB	*myeloblastosis*
NAM	*No apical meristem*
NCBI	National Center for Biotechnology Information
NUE	Nitrogen use efficient
PCR	Polymerase chain reaction
PDIL	*Protein disulfide isomerase-like gene*
PEPC-k	*Phosphoenol pyruvate carboxykinase*
PEPRKs	*Proline-rick extension-like receptor kinase*
PgNHX1	*Pennisetum glaucum* sodium hydrogen exchanger
PHL1	PHR1-*like1*
PHR1	*Phosphate starvation response1*
PK	*Pyruvate dikinase*
PP2C	*Protein phosphatase 2C.*
PPDK	*Pyruvate dikinase*
pPin 35S	Antifungal protein
QTL	Quantitative trait locus/loci
RAPD	Random amplified polymorphic DNA
RBCS	*Rubisco; PEPC, Phosphoenol pyruvate carboxylase*
rd29A	*Desiccation-responsive protein 29A*
rd29B	*Desiccation-responsive protein 29B*
RGAP2	*Rho GTase activating protein 2*
RSLP	*RNase S-like protein precursor*
SNP	Single nucleotide polymorphism;
SnRK1	*Sucrose-nonfermentation1-related protein kinase1*
SOD	*Superoxide dismutase*
SPS	*Sucrose phosphate synthase*
SRAP	Sequence-related amplified polymorphism
SSR	Simple sequence repeat
TFs	Transcription factors
TILLING	Targeting Induced Local Lesions IN Genomes
TKL	*Transketolase proteins*
TPC1	*Two pore calcium channel protein 1*
Zn	Zinc

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